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THE URAL ROCKY—MOUNTAIN-STEPPE SUBENDEMIC *Dianthus acicularis* FISCH. EX LDB.: ONTOGENY AND POPULATION DYNAMICS*

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The authors studied the biomorph, ontogenetic phases, ecological peculiarities, life strategy, and the structure and dynamics of populations of one of the characteristic rocky—mountain-steppe plants of the Urals. The significance of populations' density index and age structure for diagnosing their condition and predicting further changes was shown.

Dianthus acicularis Fisch. ex Ldb. is a typical representative of the group of rocky—mountain-steppe endemic plants of the Urals. It is not an endemic in the strict sense of the term, but a subendemic, since, besides its main Ural range, there is a fragment of the range in the Kazak low-hill region and the adjacent territory of Western Siberia. However, the center of the species' abundance is undoubtedly in the Urals, while the taxonomic position of the race growing in Kazakhstan and in Western Siberia remains debatable (M. V. Klokov planned to describe it under the name *D. toboliensis*). *D. acicularis* is found intermittently, since it is closely connected with a rocky substrate and weathering products of various rocks. Its habitats are numerous in the Southern Urals, where it grows in rocky mountain steppes and on cliffs; in the Central and Northern Urals it is found somewhat less often, on outcrops of limestone and other rocks along river banks and on exposed dunite and gabbro near the upper forest boundary (Gorchakovskii, 1969).

Our investigations were conducted in the Northern and Central Urals from 1979 through 1993 in model populations reflecting a diversity of biotopes, on sample areas 100 m^2 in size, broken up into squares of 1 m^2 each. In each square, we recorded all individuals of the given species, with their distribution by age states. Individuals were marked, and we noted the appearance of new individuals, their transition from one age state to another, and death. To characterize the populations, we used indices of the ratio of age groups and the density index (the number of individuals per 1 m^2); in the age spectra, subsenile individuals were combined with senile ones.

ONTOGENY

In the initial stage of formation of a *D. acicularis* individual (Fig. 1), plantlets (pl) have a thin rootlet and a short hypocotyl crowned with two inverted-egg-shaped or lanceolate cotyledons 4-5 mm long and 1 mm wide. The epicotyl, which appears later, bears two pairs of comparatively wide initial leaves, and then several pairs of acicular leaves similar to those on adult plants, but differing only in their somewhat smaller size.

For the first 3-5 years of the plant's life, the main shoot still grows monopodially; on juvenile (j) individuals first-order lateral shoots appear first from axillary buds of the cotyledons and initial leaves, and later from buds in the axils of acicular leaves. The main parent shoot soon lies down; its tip dies back; and the growth of shoots is subsequently accomplished sympodially. The lateral shoots also lie down. From them, the base of future skeletal axes gradually forms: plagiotropic perennial shoots lying on the substrate and then rising up.

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Fig. 1. Age states of *Dianthus acicularis*: pl) plantlets, j) juvenile, im) immature, g_1) young generative, g_2) middle-aged generative, g_3) old generative, ss) subsenile, s) senile.

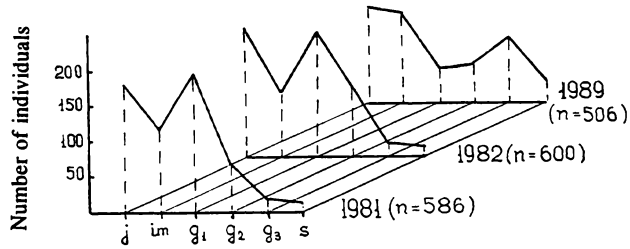

Fig. 2. Dynamics of the "Kos'vinskii Kamen" population (by years of observations: n — total number of individuals of all age states per 100 m^2).

Immature (im) individuals are already beginning to acquire features characteristic of the life form of cushion dwarf semishrubs. They have several radially arranged, more or less branched, skeletal, axial shoots. The young parts of them are densely foliated; the old parts are slightly lignified, with traces of dead leaves. The root is slightly branched, going deep into cracks in the rocks.

On young generative (g_1) individuals, a multitipped stem-root (caudex) begins to form, and the root reaches into the soil; therefore, the lower part of the skeletal shoots is covered by a layer of fine earth, and also by mosses, lichens, and dead leaves. The root itself becomes bigger and more branched. Skeletal shoots have already been formed, but they are still not branched or are slightly branched. There are a few generative shoots (usually from 1 to 10 of them) with single flowers.

On middle-aged generative (g_2) individuals, traits characteristic of the life form of stem-root cushion dwarf semishrubs that form a caudex are fully manifested. Both the vegetative and generative spheres reach their maximum development. The caudex is clearly expressed; the root is thickened; and the skeletal branches are longer, thicker, and multiply branched. The cushions reach a width of 15-20 cm and height (not counting generative shoots) of 6-10 cm. Vegetative shoots with close internodes are densely foliated (usually with 8-10 acicular leaves up to 3 cm long); the annual increment is only a few millimeters. Thanks to repeated branching, the shoots are arranged in levels. Past years' dead leaves do not fall off for a long time (staying for as long as 2-5 years), which makes the cushion very dense. Generative shoots are numerous (from 4-6 up to 60), single-, as well as double-flowered, and the number of internodes is from 3-4 up to 6. Generative shoots exist for just one year. After they finish blooming and dissemination, they die back, and shoots of subsequent orders appear from lateral (axillary) buds, producing only leaves for 2-3 years, after which new generative shoots may appear on them. There are dormant buds on the old parts of branches; in favorable conditions, some of them start to grow, which makes the cushion even denser.

Old generative (g_3) individuals (see Fig. 1) have an even thicker caudex. Death of aboveground shoots predominates over new formation of them. There are many dead shoots that do not have leaves, therefore the cushion becomes looser. The number of generative shoots may be as many as for middle-aged individuals, or somewhat lower. Generative shoots have one or two flowers and 3-4 (5) internodes; the number of shoots is from 1-2 up to 10, occasionally more.

The vegetative sphere of **subsenile (ss) individuals** is still preserved, though there are many dead and decaying shoots. The generative function is lost; sometimes there are one or two generative shoots, but with underdeveloped flowers that do not produce seeds.

Senile (s) individuals are characterized by death and decay of the greater part of the skeletal branches. Only a few, half-dead, basal parts of skeletal branches remain, with vegetative shoots mostly originating from dormant buds. There are no generative shoots.

POPULATION CHARACTERISTICS

The diversity of habitats of *D. acicularis* and peculiarities of the populations' age structure (in its dynamics) can be traced on the example of seven model populations. The names of the populations are given according to the place where they are located.

"Kos'vinskii Kamen" Population (Fig. 2). Northern Urals, 800 m above sea level, above the upper forest boundary, dunite ledge of Kos'vinskii Kamen Mountain. Dunites contain a lot of Fe, Mg, Cr, Ni, and Co; they weather rapidly, and their weathering products are easily permeable for water and quickly lose moisture. The weathering crust is continuously being

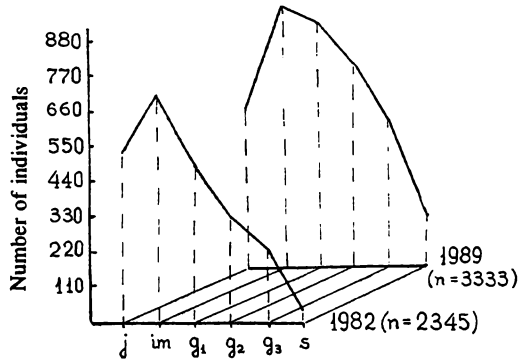

Fig. 3. Dynamics of the "Yudinskii" population.

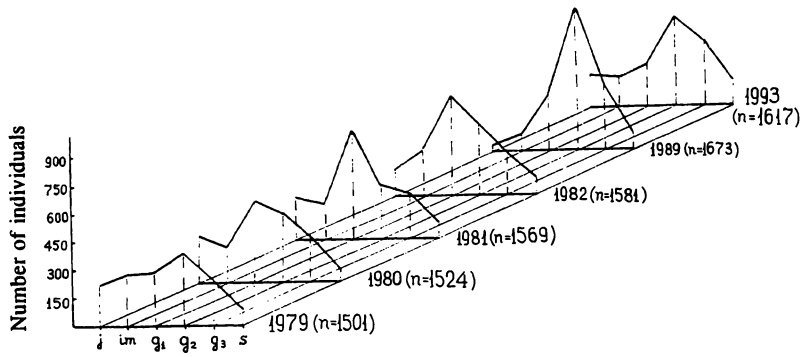

Fig. 4. Dynamics of the "Rezh serpentinite" population.

renewed. The plant cover is sparse (coverage 15%). Besides the predominant *D. acicularis*, it includes species characteristic of mountain tundras: *Festuca ovina* ssp. *ruprechtii, Scorzonera ruprechtiana, Silene acaulis, Alyssum biovulatum, Saussurea uralensis, Cerastium igoschinae*, and *Thymus pseudalternans*. This population is a normal, full-membered one; the density index is 5-5.8. In the first years of observations (1981 and 1982), the age spectrum was two-peaked, with a predominance of juvenile and young generative individuals. In 1989, old individuals were predominant in the generative generation, and the portion of senile individuals had risen; the spectrum is characterized by superposition of two waves: a descending one (death of the old generation) and an ascending one (appearance of young individuals).

"Yudinskii" Population (Fig. 3). Foot of Kos'vinskii Kamen Mountain near Yudinskii settlement (a former placer mine), very steep (40°) south slope, old dunite dump where a dredge operated. *D. acicularis* is dominant (coverage up to 40-50%); the plants occupy accumulations of fine earth between the gravel. Of other species, only *Thymus pseudalternans* is occasionally found. This population is also full-membered, but with very high density (index 23.4-33.3). The age spectrum is left-handed, of the invasive type, with significant predominance of juvenile and immature individuals. During the seven-year observation period (from 1982 through 1989), the population's density rose somewhat; there were no significant changes in its structure; and the portion of senile individuals increased a little.

"Rezh Serpentinite" Population (Fig. 4). Central Urals, Rezh River, near the place where the Glinka River empties into it, outcrop of serpentinites, very steep (45°) southeast slope, subjected to heavy erosion. Besides *D. acicularis*, there are no other species of vascular plants; coverage is up to 20%. The population is a normal, full-membered one; the density index is 15-16.7. During the observation period, only slight changes in density occurred. From 1979 through 1982, young generative individuals predominated; in 1989, the maximum shifted toward middle-aged generative individuals; and in 1993 a trend toward rejuvenation of the population was noted, which was indicated by an increase in the portion of juvenile and immature individuals. On the whole, the population's development occurred calmly; the succession of generations was accomplished slowly and gradually; and no stressful situations arose.

"Rezh Porphyrite" Population (Fig. 5). It is located in the same place as the preceding one, but the substrate is different: outcrops of basaltic porphyrites, with accumulations of grass and clay fine earth between blocks. The slope is

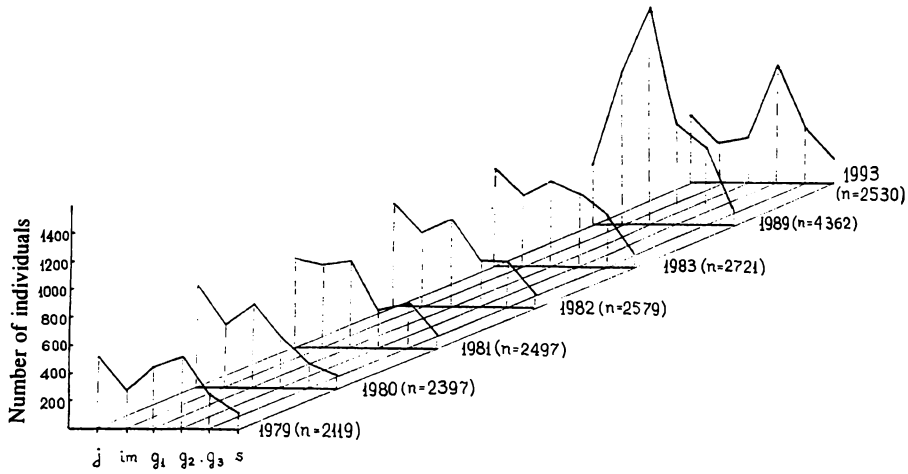

Fig. 5. Dynamics of the "Rezh porphyrite" population.

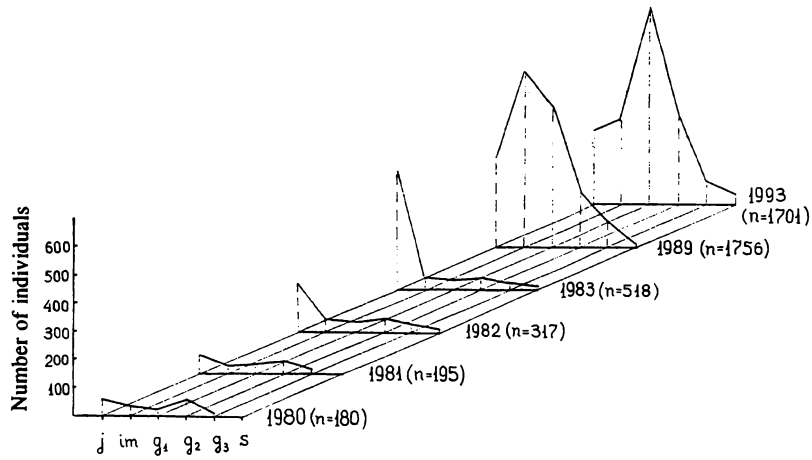

Fig. 6. Dynamics of the "Rezh clay" population.

southeast; 30° steepness. *D. acicularis* is the sole species of vascular plant here; coverage reaches 50%. The population is a normal, full-membered one; the density index is 21.2-43.6. In the first year of observations (1979), the age spectrum was two-peaked, with a maximum of juvenile and middle-aged generative individuals (the initial stage of the population's rejuvenation). In subsequent years (1980-1983), the rejuvenation trend intensified, and the number of young generative individuals began to exceed the number of middle-aged ones. As before, the spectrum remained two-peaked. In 1989, the population reached its greatest density (index 4.3) and was a normal, full-membered population with a single-peaked age spectrum, where young generative individuals account for the maximum. In 1993, the density decreased, and the age spectrum acquired two peaks, one of juvenile and one of middle-aged generative individuals, which indicates superposition of two waves, descending and ascending. During the observation period, a cycle of generations was almost completely accomplished in this population.

"Rezh Clay" Population (Fig. 6). It is located not far from the two preceding ones. It occupies a fairly gently sloping (10-15°) southeast slope, on which a layer of clay fine earth has accumulated, formed as a result of weathering of basaltic porphyrites, with a slight admixture of fine gravel. The process of formation of plant cover of grasses and forbs has begun on the slope. Besides *D. acicularis*, the grass stand's composition includes *Festuca ovina, Poa angustifolia, Sedum hybridum, Artemisia sieversiana, Berteroa incana, Scleranthus annus, Pimpinella saxifraga, Potentilla argentea*, and others. During the observation period, *D. acicularis* gradually intruded into the composition of the forming grass-forbs community. In 1980, the population density was still very low (index 1.8); the age spectrum was not full-membered; there were no senile individuals. All the way up until 1982, there was a gradual increase in the number of juvenile individuals, and the density index rose to 5.2. In 1989, immature individuals already began to predominate, and the density apparently reached the maximum possible

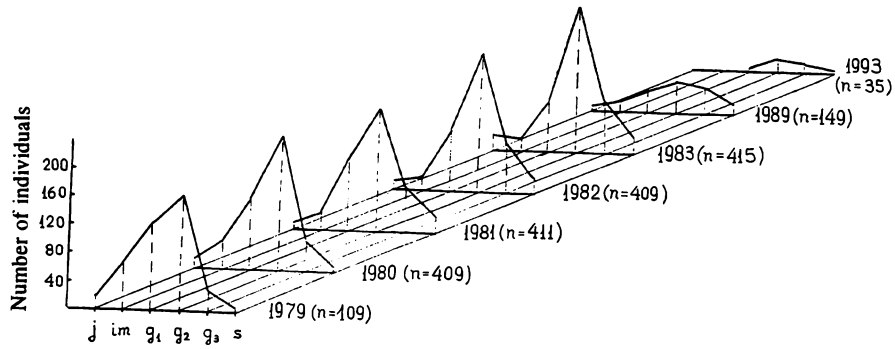

Fig. 7. Dynamics of the "Staropyshinskii" population.

level in a grass-forbs community (index 17.5). In 1993, the population became a normal, full-membered one with a single-peaked age spectrum, the maximum of which is made up of young generative individuals.

"Staropyshminskii" Population (Fig. 7). Central Urals, right bank of the Pyshma River near Staropyshminskii settlement, outcrops of serpentinites, gentle southwest slope. As a result of long weathering, a layer of fine gravel and fine earth has accumulated on the slope. The herbaceous layer is well developed; projective coverage is as much as 70%. Besides *D. acicularis*, it includes *Antennaria dioica, Luzula pallescens, Galium verum, Koeleria cristata, Festuca ovina, Veronica spicata, Polygonatum officinale, Aster alpinus, Vincetoxicum stepposum, Solidago virgaurea*, and others. The slope is being overgrown by young pine. During the period from 1979 through 1982, the population was a normal, full-membered one; the age spectrum had a peak of middle-aged generative individuals; and the density was low (index 4.0). Then, in connection with the invasion of young pine, the population began to regress, and its density dropped significantly. In 1993, when only 35 individuals remained on an area of 100 m^2, the population had almost completely collapsed, and there were no young (juvenile and immature) plants in its composition.

"Smolinskaya" Population (Fig. 8). Central Urals, limestone outcrops on the Iset River near the Smolinskie caves, in the vicinity of the "Metallurg" resort near Kamensk-Uralskii. The slope is fairly steep (15-20°), with a southeast orientation; fine earth has accumulated only in cracks and, in places, on limestone blocks. Besides *D. acicularis, Minuartia krascheninnikovii, Elytrigia pruinifera, Agropyron cristatum, Poa angustifolia, Erysimum hieracifolium, Veronica spicata, Thalictrum foetidum, Potentilla argentea, Galium verum, Polygala sibirica, Medicago falcata*, and other species grow here. Even in this case, the population is a normal, full-membered one; its density is low (index 2.8-8.1). At the beginning of the observations (1979-1980), the age spectrum was left-handed, with a peak of immature individuals. From 1980 through 1982, the population was rejuvenated, and juvenile individuals began to predominate. In 1989, the generative generation was well represented in the population, although immature individuals predominated; the density index rose to 6.7. By 1993, a normal population had formed (density index 8.1), with a peak in the age spectrum made up of middle-aged generative individuals.

CONCLUSION

Analysis of the ontogeny and morphological traits of *Dianthus acicularis* provides a basis for classifying this plant in the life form of stem-root dwarf semishrubs that form a caudex. Entry of the lower, perennial part of shoots into the soil (one of the properties of the caudex), coverage of them with a layer of fine earth, mosses, lichens, and fallen leaves, and preservation of old dead leaves for several years on vegetative shoots help to protect viable regeneration buds from drying out and promote the survival of this plant on cliffs in conditions of severe winters with thin snow cover, and sharp fluctuations of temperature and moistening conditions in the summertime.

I. V. Borisova (1962), who conducted investigations in Northern Kazakhstan, claimed that there are two life forms of *D. acicularis*: one transitional from perennial herbaceous plants to dwarf semishurbs, and one loose-cushion form. However, the photographs included in her article as an example indicate that she is actually talking not about different life forms, but about plants belonging to the same life form, but in different age states. As far as the density of the cushion, it can differ depending on the age of the plants and the nature of the substrate.

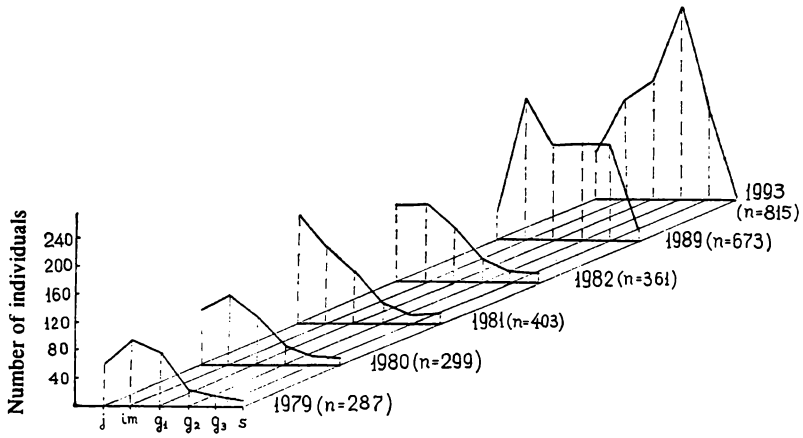

Fig. 8. Dynamics of the "Smolinskaya" population.

In the Northern and Central Urals, *D. acicularis* grows on outcrops and weathering products of various rocks: limestones, diabase porphyrites, serpentinites, and dunites. The discontinuity of its occurrence and its existence in the form of small, isolated populations are explained by the fact that such rocky outcrops are found not nearly everywhere, more often along river banks and in high mountains.

D. acicularis grows in places where competition on the part of other plants is weakened or entirely absent: on more or less steep, rocky and gravelly slopes where the substrate is continuously renewed as a result of weathering, and fine earth is intensively washed out. It also colonizes technogenic substrates, acting there in the role of a pioneer plant (the formation of the population of it on dunite dumps of the Yudinskii mine serves as an example). However, as fine-earth material accumulates on slopes and they are colonized by other plants, populations of *D. acicularis* degrade, which could be observed, in particular, on the bank of the Pyshma River near Staropyshminskii. Thus, *D. acicularis*, like other Ural endemic rocky—mountain-steppe plants that we have studied previously (Gorchakovskii and Zueva, 1984, 1993; Gorchakovskii and Stepanova, 1994), is classified according to its life strategy as an explerent (Ramenskii, 1971, or an R strategist (Grime, 1979).

The density of *D. acicularis* populations varies significantly, depending on their condition and habitat. Increased values of the density index (33) were noted in a population of the invasive type on dunite dumps of an abandoned dunite mine (on account of a predominance of juvenile and immature individuals). This index was fairly high (up to 15-25, less often as much as 43) in mature populations formed on steep slopes of river cliffs, where interspecific competition is reduced to a minimum. In the rest of the cases, in the initial stages of the populations' formation, as well as when they are dying out, in conditions of increasing interspecific competition the populations' density index is significantly lower.

Changes in the age structure of the populations that we studied are of a wave nature, with superposition of two waves usually being observed: a descending one (death of the old generation) and an ascending one (introduction of a young generation). In contrast to some other Ural rocky—mountain-steppe endemics, *Onosma guberlinensis* for example, the population dynamics of *D. acicularis* depends less on the meteorological situation of individual years and is mainly determined by endogenous factors (which is partly connected with the longer life span of this plant). Judging from our observations, where interspecific competition is ruled out and there are no exogenous disturbances, the cycle of generations in *D. acicularis* populations is accomplished over the course of approximately 14-15 years.

The density index and age structure can be used successfully within a framework of phytomonitoring to diagnose the condition of populations of endemic plants and predict further changes in them.

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